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Micromechanics of root development in soil

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Keywords: plant roots, particle, granular media, biomechanics

Abstract

Our understanding of how root develop in soil may be at the eve of significant transformations. The formidable expansion of imaging technologies enables live observations of the rhizosphere micro-pore architecture at unprecedented resolution. Granular matter physics provides ways to understand the microscopic fluctuations of forces in soils, and the increasing knowledge of plant mechanobiology may shed new lights on how roots perceive soil heterogeneity. This opinion paper exposes how recent scientific achievements may contribute to design a new theory for root growth in heterogeneous environments.

Main text

Current knowledge of the biomechanics of plant root growth in soil is largely based on the extensive work of plant biophysicists from the second half of the 20th century { ADDIN EN.CITE { ADDIN

EN.CITE.DATA }} . The view was that both roots and soil must be considered as continua so that the description of root soil interactions can be achieved with continuous mathematical functions of macroscopic variables such as Young’s modulus of root tissue, soil penetration stress, and pore water pressure { ADDIN EN.CITE <EndNote><Cite><Author>Abdalla</Author><Year>1969</Year><RecNum>232</RecNum><DisplayText>[4]</DisplayText><record><rec-number>232</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512665632">232</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Abdalla, AM</author><author>Hettiaratchi, DRP</author><author>Reece, AR</author></authors></contributors><titles><title>The mechanics of root growth in granular media</title><secondary-title>Journal of Agricultural Engineering Research</secondary-title></titles><periodical><full-title>Journal of Agricultural Engineering Research</full-title></periodical><pages>236-248</pages><volume>14</volume><number>3</number><dates><year>1969</year></dates><isbn>0021-8634</isbn><urls></urls></record></Cite></EndNote>}. Classical concepts from mechanics and physiology then provide a suitable framework to understand factors controlling tissue growth in its natural environment. The energy required to deform the root and surrounding soil, which originates from the photosynthetic chemical energy accumulated within the tissues, is converted into turgor pressure and mechanical energy { ADDIN EN.CITE <EndNote><Cite><Author>Silk</Author><Year>1980</Year><RecNum>229</RecNum><DisplayText>[5]</DisplayText><record><rec-number>229</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512664575">229</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Silk, W. K.</author><author>Wagner, K.</author></authors></contributors><titles><title>Growth-sustaining water potential distributions in the primary corn root. a non compartmented continuum model</title><secondary-title>Plant Physiology</secondary-title></titles><periodical><full-

title>Plant Physiology</full-title></periodical><pages>859-863</pages><volume>66</volume><number>5</number><dates><year>1980</year></dates><isbn>1532-2548</isbn><urls></urls></record></Cite></EndNote>}. Turgor pressure then overcome the resistance from cell wall to stretching, the resistance to movement of water across membranes, and the resistance to the displacement of the soil around the root { ADDIN EN.CITE <EndNote><Cite><Author>Dexter</Author><Year>1987</Year><RecNum>226</RecNum><DisplayText>[6]</DisplayText><record><rec-number>226</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512663998">226</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Dexter, AR</author></authors></contributors><titles><title>Mechanics of root growth</title><secondary-title>Plant and soil</secondary-title></titles><periodical><full-title>Plant and Soil</full-title></periodical><pages>303-312</pages><volume>98</volume><number>3</number><dates><year>1987</year></dates><isbn>0032-079X</isbn><urls></urls></record></Cite></EndNote>}.

This classical view of root-soil biomechanics has been central to identify the biophysical factors limiting growth in soil, but it is now challenged to predict morphologies and developmental patterns observed in natural conditions (Figure 1). If roots were to experience homogeneous mechanical stress from the soil, one would expect turgor pressure and Lockhart equation { ADDIN EN.CITE <EndNote><Cite><Author>Lockhart</Author><Year>1965</Year><RecNum>185</RecNum><DisplayText>[1]</DisplayText><record><rec-number>185</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512051649">185</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Lockhart, James A</author></authors></contributors><titles><title>An analysis of irreversible plant cell elongation</title><secondary-title>Journal of Theoretical Biology</secondary-title></titles><periodical><full-title>Journal of theoretical biology</full-title></periodical><pages>264-

275</pages><volume>8</volume><number>2</number><dates><year>1965</year></dates><isbn>0022-5193</isbn><urls></urls></record></Cite></EndNote>**}** to predict accurately growth arrest in soil. This is not the case and large discrepancies remain between measured turgor pressure (in the order of 1MPa **{** ADDIN EN.CITE <EndNote><Cite><Author>Clark</Author><Year>1996</Year><RecNum>231</RecNum><DisplayText>[7]</DisplayText><record><rec-number>231</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512664911">231</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Clark, LJ</author><author>Whalley, WR</author><author>Dexter, AR</author><author>Barraclough, PB</author><author>Leigh, RA</author></authors></contributors><titles><title>Complete mechanical impedance increases the turgor of cells in the apex of pea roots</title><secondary-title>Plant, Cell & Environment</secondary-title></titles><periodical><full-title>Plant, Cell & Environment</full-title></periodical><pages>1099-1102</pages><volume>19</volume><number>9</number><dates><year>1996</year></dates><isbn>1365-3040</isbn><urls></urls></record></Cite></EndNote>**}**) and the levels of mechanical stresses at which growth is arrested (>5MPa **{** ADDIN EN.CITE <EndNote><Cite><Author>Bengough</Author><Year>1991</Year><RecNum>224</RecNum><DisplayText>[8]</DisplayText><record><rec-number>224</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512663558">224</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Bengough, AG</author><author>Mullins, CE</author></authors></contributors><titles><title>Penetrometer resistance, root penetration resistance and root elongation rate in two sandy loam soils</title><secondary-title>Plant and Soil</secondary-title></titles><periodical><full-title>Plant and Soil</full-title></periodical><pages>59-66</pages><volume>131</volume><number>1</number><dates><year>1991</year></dates><isbn>0032-079X</isbn><urls></urls></record></Cite></EndNote>**}**). Classical mechanics of continua is illequipped to explain the links between soil heterogeneity and stochasticity of plant development. The root tissue itself is heterogeneous and cell types have different roles in facilitating growth and penetration. Anchoring the base of the root for example, is necessary for cell elongation to produce apical movement and deformation of the soil { ADDIN EN.CITE <EndNote><Cite><Author>Bengough</Author><Year>2016</Year><RecNum>225</RecNum><DisplayText>[9]</DisplayText><record><rec-number>225</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512663688">225</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Bengough, A Glyn</author><author>Loades, Kenneth</author><author>McKenzie, Blair M</author></authors></contributors><titles><title>Root hairs aid soil penetration by anchoring the root surface to pore walls</title><secondary-title>Journal of Experimental Botany</secondary-title></titles><periodical><full-title>Journal of experimental botany</full-title></periodical><pages>1071-1078</pages><volume>67</volume><number>4</number><dates><year>2016</year></dates><isbn>0022-0957</isbn><urls></urls></record></Cite></EndNote>}. The root cap and its associated border cells have also a fundamental role in reducing friction from the bulk soil. It was shown recently that wheat genotypes with sharper root tips are more efficient at soil penetration { ADDIN EN.CITE <EndNote><Cite><Author>Colombi</Author><Year>2017</Year><RecNum>230</RecNum><DisplayText>[10]</DisplayText><record><rec-number>230</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512664744">230</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Colombi, Tino</author><author>Kirchgessner, Norbert</author><author>Walter, Achim</author><author>Keller, Thomas</author></authors></contributors><titles><title>Root tip shape governs root elongation rate under increased soil strength</title><secondary-title>Plant Physiology</secondary-title></titles><periodical><full-title>Plant Physiology</full-title></periodical><pages>2289-

2301</pages><volume>174</volume><number>4</number><dates><year>2017</year></dates><isbn>0032-0889</isbn><urls></urls></record></Cite></EndNote>**}**.

To establish a biomechanical framework that accounts for the complexity of root interactions with the granular medium, one must capture the microscopic nature of particle forces and the collective action they have on root tissues (Figure 1A). **{** ADDIN EN.CITE <EndNote><Cite AuthorYear="1"><Author>Evelyne</Author><Year>2017</Year><RecNum>199</RecNum><DisplayText>Kolb, et al. [11]</DisplayText><record><rec-number>199</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512484212">199</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Kolb, Evelyne</author><author>Legue, Valérie</author><author>Bogeat-Triboulot, Marie-Béatrice</author></authors></contributors><titles><title>Physical root-soil interactions</title><secondary-title>Physical Biology</secondary-title></titles><periodical><full-title>Physical biology</full-title></periodical><pages>065004</pages><volume>14</volume><dates><year>2017</year></dates><isbn>1478-3975</isbn><urls></urls></record></Cite></EndNote>**}** proposed to categorise the nature of root mechanical responses to soil based on the scale of the soil heterogeneities. When the medium is composed of small particles, individual variations in the force required to move them are not perceived by the root. The behaviour of roots and soil can be homogenised, and classical continuum mechanics usually applies (Box 1A) **{** ADDIN EN.CITE <EndNote><Cite><Author>Faure</Author><Year>1994</Year><RecNum>233</RecNum><DisplayText>[12]</DisplayText><record><rec-number>233</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512665757">233</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Faure, AG</author></authors></contributors><titles><title>Stress field developed by root growth: theoretical approach</title><secondary-title>Journal of Agricultural Engineering

Research</secondary-title></titles><periodical><full-title>Journal of Agricultural Engineering Research</full-title></periodical><pages>53-67</pages><volume>58</volume><number>1</number><dates><year>1994</year></dates><isbn>0021-8634</isbn><urls></urls></record></Cite></EndNote>}. Soils also contain objects that are too large and or too rigid for a root to deform and displace, for example when roots grow in contact with stones, in cracks or pores { ADDIN EN.CITE <EndNote><Cite><Author>Jackson</Author><Year>1999</Year><RecNum>234</RecNum><DisplayText>[13,14]</DisplayText><record><rec-number>234</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512725012">234</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Jackson, RB</author><author>Moore, LA</author><author>Hoffmann, WwA</author><author>Pockman, WT</author><author>Linder, CR</author></authors></contributors><titles><title>Ecosystem rooting depth determined with caves and DNA</title><secondary-title>Proceedings of the National Academy of Sciences of the United States of America</secondary-title></titles><periodical><full-title>Proceedings of the National Academy of Sciences of the United States of America</full-title></periodical><pages>11387-11392</pages><volume>96</volume><number>20</number><dates><year>1999</year></dates><isbn>0027-8424</isbn><urls></urls></record></Cite><Cite><Author>White</Author><Year>2010</Year><RecNum>235</RecNum><record><rec-number>235</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512725591">235</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>White, Rosemary G</author><author>Kirkegaard, John A</author></authors></contributors><titles><title>The distribution and abundance of wheat roots in a dense, structured subsoil–implications for water uptake</title><secondary-title>Plant, Cell & Environment</secondary-title></titles><periodical><full-title>Plant, Cell & Environment</full-

title></periodical><pages>133-148</pages><volume>33</volume><number>2</number><dates><year>2010</year></dates><isbn>1365-3040</isbn><urls></urls></record></Cite></EndNote>}. Growth forces cannot displace the obstacle and the root usually combines tropic responses and mechanical buckling to avoid the obstacle (Box 1B) { ADDIN EN.CITE <EndNote><Cite><Author>Monshausen</Author><Year>2009</Year><RecNum>200</RecNum><DisplayText>[15]</DisplayText><record><rec-number>200</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512484654">200</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Monshausen, Gabriele B</author><author>Gilroy, Simon</author></authors></contributors><titles><title>The exploring root—root growth responses to local environmental conditions</title><secondary-title>Current opinion in plant biology</secondary-title></titles><periodical><full-title>Current opinion in plant biology</full-title></periodical><pages>766-772</pages><volume>12</volume><number>6</number><dates><year>2009</year></dates><isbn>1369-5266</isbn><urls></urls></record></Cite></EndNote>}. The behaviour of roots growing in soils with particles of intermediate sizes is more challenging to understand. A root can displace individual particles from the soil, but the forces exerted by each of the particles can also influence the course of root development (Box 1C). Although such growth environments are common for fine roots or due to the presence of aggregate and sand particles, growth patterns in such conditions are not well understood. How frequently does a root deflect from their growth trajectory? What are the magnitude of deflections? How does the distribution of particle forces modify the growth trajectory?

Understanding the forces acting on a root during the elongation requires detailed knowledge of the physics of granular media. Granular media are assemblages of particles held by frictional and repulsive forces from adjacent particles. The forces holding particles together form chain-like networks that propagate at the contact points between neighbouring particles { ADDIN EN.CITE

<EndNote><Cite><Author>Mueth</Author><Year>1998</Year><RecNum>236</RecNum><DisplayText>[16]</DisplayText><record><rec-number>236</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512726253">236</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Mueth, Daniel M</author><author>Jaeger, Heinrich M</author><author>Nagel, Sidney R</author></authors></contributors><titles><title>Force distribution in a granular medium</title><secondary-title>Physical Review E</secondary-title></titles><periodical><full-title>Physical Review E</full-title></periodical><pages>3164-3169</pages><volume>57</volume><number>3</number><dates><year>1998</year></dates><urls></urls></record></Cite></EndNote>**}**. Because particles are disordered or have various sizes and shapes, large variations in magnitude and direction of particle forces arise **{** ADDIN EN.CITE <EndNote><Cite><Author>Mueth</Author><Year>1998</Year><RecNum>236</RecNum><DisplayText>[16,17]</DisplayText><record><rec-number>236</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512726253">236</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Mueth, Daniel M</author><author>Jaeger, Heinrich M</author><author>Nagel, Sidney R</author></authors></contributors><titles><title>Force distribution in a granular medium</title><secondary-title>Physical Review E</secondary-title></titles><periodical><full-title>Physical Review E</full-title></periodical><pages>3164-3169</pages><volume>57</volume><number>3</number><dates><year>1998</year></dates><urls></urls></record></Cite><Cite><Author>Liu</Author><Year>1995</Year><RecNum>237</RecNum><record><rec-number>237</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512726482">237</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Liu, CH</author><author>Nagel, Sydney R</author><author>Schecter, DA</author><author>Coppersmith, SN</author><author>Majumdar,

Satya</author></authors></contributors><titles><title>Force fluctuations in bead packs</title><secondary-title>Science</secondary-title></titles><periodical><full-title>Science</full-title></periodical><pages>513-515</pages><volume>269</volume><number>5223</number><dates><year>1995</year></dates><isbn>0036-8075</isbn><urls></urls></record></Cite></EndNote>**}**. Early theoretical work based on dry and static monodisperse particles showed that distribution of contact forces vary greatly and the overall force distribution follows an exponential decline **{** ADDIN EN.CITE <EndNote><Cite><Author>Coppersmith</Author><Year>1996</Year><RecNum>186</RecNum><DisplayText>[18,19]</DisplayText><record><rec-number>186</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512053975">186</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Coppersmith, SN</author><author>Liu, C-h</author><author>Majumdar, Satya</author><author>Narayan, Onuttom</author><author>Witten, TA</author></authors></contributors><titles><title>Model for force fluctuations in bead packs</title><secondary-title>Physical Review E</secondary-title></titles><periodical><full-title>Physical Review E</full-title></periodical><pages>4673-4685</pages><volume>53</volume><number>5</number><dates><year>1996</year></dates><urls></urls></record></Cite><Cite><Author>Hurley</Author><Year>2016</Year><RecNum>251</RecNum><record><rec-number>251</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1513158087">251</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Hurley, RC</author><author>Hall, SA</author><author>Andrade, JE</author><author>Wright, J</author></authors></contributors><titles><title>Quantifying interparticle forces and heterogeneity in 3D granular materials</title><secondary-title>Physical Review Letters</secondary-title></titles><periodical><full-title>Physical Review Letters</full-title></periodical><pages>098005</pages><volume>117</volume><number>9</number><dates><

year>2016</year></dates><urls></urls></record></Cite></EndNote>}. Particles dynamics is better understood too. Contact forces in granular media propagate through complex waves { ADDIN EN.CITE <EndNote><Cite><Author>Zhang</Author><Year>2017</Year><RecNum>61</RecNum><DisplayText>[20]</DisplayText><record><rec-number>61</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1511963947">61</key><key app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Zhang, Lingran</author><author>Lambert, Stéphane</author><author>Nicot, François</author></authors></contributors><titles><title>Discrete dynamic modelling of the mechanical behaviour of a granular soil</title><secondary-title>International Journal of Impact Engineering</secondary-title></titles><periodical><full-title>International Journal of Impact Engineering</full-title></periodical><pages>76-89</pages><volume>103</volume><section>76</section><dates><year>2017</year></dates><isbn>0734743X</isbn><urls></urls><electronic-resource-num>10.1016/j.ijimpeng.2017.01.009</electronic-resource-num></record></Cite></EndNote>} with appearance of macroscopic phenomenon such as clogging and arching, where particles spontaneously organise as vaults { ADDIN EN.CITE <EndNote><Cite><Author>Aranson</Author><Year>2006</Year><RecNum>191</RecNum><DisplayText>[21]</DisplayText><record><rec-number>191</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512054913">191</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Aranson, Igor S</author><author>Tsimring, Lev S</author></authors></contributors><titles><title>Patterns and collective behavior in granular media: Theoretical concepts</title><secondary-title>Reviews of Modern Physics</secondary-title></titles><periodical><full-title>Reviews of modern physics</full-title></periodical><pages>641-692</pages><volume>78</volume><number>2</number><dates><year>2006</year></dates><urls

></urls></record></Cite></EndNote>**}**. Solid, liquid and even gaseous phases may be observed in granular media depending on the external forces applied upon them **{** ADDIN EN.CITE <EndNote><Cite><Author>Gnoli</Author><Year>2016</Year><RecNum>202</RecNum><DisplayText>[22]</DisplayText><record><rec-number>202</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512485408">202</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Gnoli, Andrea</author><author>Lasanta, Antonio</author><author>Sarracino, Alessandro</author><author>Puglisi, Andrea</author></authors></contributors><titles><title>Unified rheology of vibro-fluidized dry granular media: From slow dense flows to fast gas-like regimes</title><secondary-title>Scientific Reports</secondary-title></titles><periodical><full-title>Scientific reports</full-title></periodical><pages>38604</pages><volume>6</volume><dates><year>2016</year></dates> <urls></urls></record></Cite></EndNote>**}**. Indeed, powerful techniques and hardware are available to examine theories in conditions that are nearly identical to experiments. 3D templates of the pore geometry together with description of the root and anatomical details can be obtained **{** ADDIN EN.CITE <EndNote><Cite><Author>Richard</Author><Year>2003</Year><RecNum>203</RecNum><DisplayText>[23,24]</DisplayText><record><rec-number>203</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512485734">203</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Richard, Patrick</author><author>Philippe, Pierre</author><author>Barbe, Fabrice</author><author>Bourlès, Stéphane</author><author>Thibault, Xavier</author><author>Bideau, Daniel</author></authors></contributors><titles><title>Analysis by x-ray microtomography of a granular packing undergoing compaction</title><secondary-title>Physical Review E</secondary-title></titles><periodical><full-title>Physical Review E</full-title></periodical><pages>020301-

1</pages><volume>68</volume><number>2</number><dates><year>2003</year></dates><urls></urls></record></Cite><Cite><Author>Vlahinić</Author><Year>2013</Year><RecNum>69</RecNum><record><rec-number>69</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1511963981">69</key><key app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Vlahinić, Ivan</author><author>Andò, Edward</author><author>Viggiani, Gioacchino</author><author>Andrade, José E.</author></authors></contributors><titles><title>Towards a more accurate characterization of granular media: extracting quantitative descriptors from tomographic images</title><secondary-title>Granular Matter</secondary-title></titles><periodical><full-title>Granular Matter</full-title></periodical><pages>9-21</pages><volume>16</volume><number>1</number><section>9</section><dates><year>2013</year></dates><isbn>1434-5021
1434-7636</isbn><urls></urls><electronic-resource-num>10.1007/s10035-013-0460-6</electronic-resource-num></record></Cite></EndNote>**}**, and there are efficient computational techniques that exploit the power of Graphical Processing Unit to simulate roots and soil at the particle and cell resolution. Discrete Element Modelling (DEM) for example uses Newton's second law to describe the motion of millions of interacting particles **{** ADDIN EN.CITE <EndNote><Cite><Author>Guo</Author><Year>2015</Year><RecNum>51</RecNum><DisplayText>[25,26]</DisplayText><record><rec-number>51</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1511963873">51</key><key app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Guo, Yu</author><author>Curtis, Jennifer Sinclair</author></authors></contributors><titles><title>Discrete Element Method Simulations for Complex Granular Flows</title><secondary-title>Annual Review of Fluid Mechanics</secondary-title></titles><periodical><full-title>Annual Review of Fluid Mechanics</full-

title></periodical><pages>21-46</pages><volume>47</volume><number>1</number><section>21</section><dates><year>2015</year></dates><isbn>0066-4189
1545-4479</isbn><urls></urls><electronic-resource-num>10.1146/annurev-fluid-010814-014644</electronic-resource-num></record></Cite><Cite><Author>Nicot</Author><Year>2017</Year><RecNum>220</RecNum><record><rec-number>220</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512646059">220</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Nicot, François</author><author>Xiong, Hao</author><author>Wautier, Antoine</author><author>Lerbet, Jean</author><author>Darve, Félix</author></authors></contributors><titles><title>Force chain collapse as grain column buckling in granular materials</title><secondary-title>Granular Matter</secondary-title></titles><periodical><full-title>Granular Matter</full-title></periodical><pages>18</pages><volume>19</volume><number>2</number><dates><year>2017</year></dates><isbn>1434-5021</isbn><urls></urls></record></Cite></EndNote>**}**. The models reproduce closely experimental observations, even in the case of biologically complex systems with detailed quantification of the force distribution surrounding growing roots **{** ADDIN EN.CITE <EndNote><Cite><Author>Bourrier</Author><Year>2013</Year><RecNum>222</RecNum><DisplayText>[27,28]</DisplayText><record><rec-number>222</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512646513">222</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Bourrier, Franck</author><author>Kneib, François</author><author>Chareyre, Bruno</author><author>Fourcaud, Thierry</author></authors></contributors><titles><title>Discrete modeling of granular soils reinforcement by plant roots</title><secondary-title>Ecological Engineering</secondary-title></titles><periodical><full-title>Ecological Engineering</full-title></periodical><pages>646-

657</pages><volume>61</volume><dates><year>2013</year></dates><isbn>0925-8574</isbn><urls></urls></record></Cite><Cite><Author>akih</Author><Year>2017</Year><RecNum>270</RecNum><record><rec-number>270</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1520156221">270</key></foreign-keys><ref-type name="Conference Proceedings">10</ref-type><contributors><authors><author>Fakih, Mahmoud</author><author>Delenne, Jean Yves</author><author>Radjai, Farhang</author><author>Fourcaud, Thierry</author></authors></contributors><titles><title>Modeling root growth in granular soils: effects of root stiffness and packing fraction</title><secondary-title>EPJ Web of Conferences</secondary-title></titles><periodical><full-title>EPJ Web of Conferences</full-title></periodical><pages>14013</pages><volume>140</volume><dates><year>2017</year></dates><publisher>EDP Sciences</publisher><isbn>2100-014X</isbn><urls></urls></record></Cite></EndNote>}.

Despite recent experimental and theoretical breakthroughs, granular matter physics has not transformed our understanding of the mechanics of root growth. Many current limitations are due to our lack of understanding of how roots respond to complex mechanical signals, and particularly how competition between multiple mechanical stimuli affects root responses. Cellular mechanisms involved in the response to physical obstacles have not been fully characterised, but a growing number of studies are now revealing the signalling and regulatory mechanisms involved in plant responses to mechanical force. Research in animal sciences have identified a multitude of proteins which binding domains are modified by mechanical forces { ADDIN EN.CITE <EndNote><Cite><Author>Iskratsch</Author><Year>2014</Year><RecNum>269</RecNum><DisplayText>[29]</DisplayText><record><rec-number>269</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1519223480">269</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Iskratsch, Thomas</author><author>Wolfenson, Haguy</author><author>Sheetz, Michael

P</author></authors></contributors><titles><title>Appreciating force and shape—the rise of mechanotransduction in cell biology</title><secondary-title>Nature Reviews Molecular Cell Biology</secondary-title></titles><periodical><full-title>Nature Reviews Molecular Cell Biology</full-title></periodical><pages>825</pages><volume>15</volume><number>12</number><dates><year>2014</year></dates><isbn>1471-0080</isbn><urls></urls></record></Cite></EndNote>**}** and their discovery in plants may follow. Large families of mechanosensitive ion channels have been identify in plants **{** ADDIN EN.CITE <EndNote><Cite><Author>Hamilton</Author><Year>2015</Year><RecNum>240</RecNum><DisplayText>[30]</DisplayText><record><rec-number>240</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512938828">240</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Hamilton, Eric S</author><author>Schlegel, Angela M</author><author>Haswell, Elizabeth S</author></authors></contributors><titles><title>United in diversity: mechanosensitive ion channels in plants</title><secondary-title>Annual Review of Plant Biology</secondary-title></titles><periodical><full-title>Annual review of plant biology</full-title></periodical><pages>113-137</pages><volume>66</volume><dates><year>2015</year></dates><isbn>1543-5008</isbn><urls></urls></record></Cite></EndNote>**}**, with for example MCA calcium mechanosensitive channels being linked to growth response to hard gel layers **{** ADDIN EN.CITE <EndNote><Cite><Author>Nakagawa</Author><Year>2007</Year><RecNum>268</RecNum><DisplayText>[31]</DisplayText><record><rec-number>268</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1519213479">268</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Nakagawa, Yuko</author><author>Katagiri, Takeshi</author><author>Shinozaki, Kazuo</author><author>Qi, Zhi</author><author>Tatsumi, Hitoshi</author><author>Furuichi, Takuya</author><author>Kishigami, Akio</author><author>Sokabe,

Masahiro</author><author>Kojima, Itaru</author><author>Sato, Shusei</author></authors></contributors><titles><title>Arabidopsis plasma membrane protein crucial for Ca2+ influx and touch sensing in roots</title><secondary-title>Proceedings of the National Academy of Sciences</secondary-title></titles><periodical><full-title>Proceedings of the National Academy of Sciences</full-title></periodical><pages>3639-3644</pages><volume>104</volume><number>9</number><dates><year>2007</year></dates><isbn>0027-8424</isbn><urls></urls></record></Cite></EndNote>**}**. Adaptation to mechanical forces are also well characterised, including the changes in cell division patterns, growth direction, cell differentiation and gene expression **{** ADDIN EN.CITE <EndNote><Cite><Author>Mirabet</Author><Year>2011</Year><RecNum>262</RecNum><DisplayText>[32]</DisplayText><record><rec-number>262</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1518712800">262</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Mirabet, Vincent</author><author>Das, Pradeep</author><author>Boudaoud, Arezki</author><author>Hamant, Olivier</author></authors></contributors><titles><title>The role of mechanical forces in plant morphogenesis</title><secondary-title>Annual review of plant biology</secondary-title></titles><periodical><full-title>Annual review of plant biology</full-title></periodical><pages>365-385</pages><volume>62</volume><dates><year>2011</year></dates><isbn>1543-5008</isbn><urls></urls></record></Cite></EndNote>**}**

A main difficulty, however, is to understand the nature of the mechanical signals perceived from the soil particles surrounding plant roots. It is central to develop capabilities to study not only the forces and displacement produced in the root soil system, but also the biological responses due to mechanical interactions with soil particles. Unfortunately, experimenting with natural soils is challenging because of its opacity. Rhizotron systems have been an extremely powerful tool to study root growth **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**, glass interfaces introduce strong border effects and observations of biomechanical processes are often biased. X-ray imaging allows visualisation of interactions between roots and soil particles *in situ* in high resolution **{** ADDIN EN.CITE <EndNote><Cite><Author>Mooney</Author><Year>2012</Year><RecNum>238</RecNum><DisplayText>[35]</DisplayText><record><rec-number>238</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512727537">238</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Mooney, Sacha J</author><author>Pridmore, Tony P</author><author>Helliwell, Jonathan</author><author>Bennett, Malcolm J</author></authors></contributors><titles><title>Developing X-ray computed tomography to non-invasively image 3-D root systems architecture in soil</title><secondary-title>Plant and soil</secondary-title></titles><periodical><full-title>Plant and Soil</full-title></periodical><pages>1-22</pages><volume>352</volume><number>1-2</number><dates><year>2012</year></dates><isbn>0032-079X</isbn><urls></urls></record></Cite></EndNote>**}**. The technique allows time-lapse imaging for several weeks of growth. Improved images can be obtained with the application of contrasting agents. For example, iodine perfused into plant leaves revealed the vascular structures of the roots and rhizobial nodules **{** ADDIN EN.CITE <EndNote><Cite><Author>Keyes</Author><Year>2017</Year><RecNum>125</RecNum><DisplayText>[36]</DisplayText><record><rec-number>125</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1511964225">125</key><key app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Keyes, S. D.</author><author>Gostling, N. J.</author><author>Cheung, J. H.</author><author>Roose, T.</author><author>Sinclair, I.</author><author>Marchant, A.</author></authors></contributors><auth-address>2The Faculty of Engineering and the Environment,The University of Southampton,Southampton,SO17 1BJ,UK.
1The Centre for Biological Sciences,The University of Southampton,Southampton,SO17

1BJ,UK.</auth-address><titles><title>The Application of Contrast Media for In Vivo Feature Enhancement in X-Ray Computed Tomography of Soil-Grown Plant Roots</title><secondary-title>Microscopy and Microanalysis</secondary-title></titles><periodical><full-title>Microscopy and Microanalysis</full-title></periodical><pages>538-552</pages><volume>23</volume><number>3</number><edition>2017/03/23</edition><keywords><keyword>X-ray computed tomography</keyword><keyword>contrast agents</keyword><keyword>imaging</keyword><keyword>plant roots</keyword></keywords><dates><year>2017</year><pub-dates><date>Jun</date></pub-dates></dates><isbn>1435-8115 (Electronic)
1431-9276 (Linking)</isbn><accession-num>28320487</accession-num><urls><related-urls><url>https://www.ncbi.nlm.nih.gov/pubmed/28320487</url></related-urls></urls><electronic-resource-num>10.1017/S1431927617000319</electronic-resource-num></record></Cite></EndNote>**}**. Root hairs can be resolved using synchrotron sources with resolution of up to 5µm and at temporal resolution sufficient for tracking particle movement due to root growth **{** ADDIN EN.CITE <EndNote><Cite><Author>Keyes</Author><Year>2017</Year><RecNum>223</RecNum><DisplayText>[37]</DisplayText><record><rec-number>223</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512646619">223</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Keyes, SD</author><author>Cooper, Laura</author><author>Duncan, S</author><author>Koebernick, N</author><author>Fletcher, DM McKay</author><author>Scotson, CP</author><author>Van Veelen, Arjen</author><author>Sinclair, Ian</author><author>Roose, Tiina</author></authors></contributors><titles><title>Measurement of micro-scale soil deformation around roots using four-dimensional synchrotron tomography and image correlation</title><secondary-title>Journal of The Royal Society Interface</secondary-title></titles><periodical><full-title>Journal of The Royal Society Interface</full-

title></periodical><pages>20170560</pages><volume>14</volume><number>136</number><dates><year>2017</year></dates><isbn>1742-5689</isbn><urls></urls></record></Cite></EndNote>**}**. However, X-ray is an ionising radiation that affects biological processes especially meristematic regions where high cell division rates occurs **{** ADDIN EN.CITE <EndNote><Cite><Author>De Micco</Author><Year>2011</Year><RecNum>239</RecNum><DisplayText>[38]</DisplayText><record><rec-number>239</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512729900">239</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>De Micco, Veronica</author><author>Arena, Carmen</author><author>Pignalosa, Diana</author><author>Durante, Marco</author></authors></contributors><titles><title>Effects of sparsely and densely ionizing radiation on plants</title><secondary-title>Radiation and Environmental Biophysics</secondary-title></titles><periodical><full-title>Radiation and Environmental Biophysics</full-title></periodical><pages>1-19</pages><volume>50</volume><number>1</number><dates><year>2011</year></dates><isbn>0301-634X</isbn><urls></urls></record></Cite></EndNote>**}**, and despite the increase in resolutions, details of the inner cellular processes and biochemical activity have remained invisible **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**.

Optics and microscopy in the visible range have thus remained the preferred approach to make observation of the biology and mechanics of the root. Confocal Laser Scanning Microscopes (CLSM) have provided the first live images of root-particle interaction in high resolution with details available on contact with particle surface, anatomical features at cell resolution and gene expression **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. FRET imaging now allows tension sensors to record molecular forces at the piconewton scale **{** ADDIN EN.CITE <EndNote><Cite><Author>Cost</Author><Year>2015</Year><RecNum>263</RecNum><DisplayText>[43]</DisplayText><record><rec-number>263</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1518798628">263</key></foreign-

keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Cost, Anna-Lena</author><author>Ringer, Pia</author><author>Chrostek-Grashoff, Anna</author><author>Grashoff, Carsten</author></authors></contributors><titles><title>How to measure molecular forces in cells: a guide to evaluating genetically-encoded FRET-based tension sensors</title><secondary-title>Cellular and molecular bioengineering</secondary-title></titles><periodical><full-title>Cellular and molecular bioengineering</full-title></periodical><pages>96-105</pages><volume>8</volume><number>1</number><dates><year>2015</year></dates><isbn>1865-5025</isbn><urls></urls></record></Cite></EndNote>**}**. However, CLSM has proved limited for long observations due to photo toxicity and photo bleaching. Because of the confined environment of the microscope, it has also remained limited to small plant samples. The field is now turning to different types of microscopes. Light Sheet Microscopy (LSM), in particular, has drastically reduced the light doses to the samples **{** ADDIN EN.CITE <EndNote><Cite><Author>Reynaud</Author><Year>2008</Year><RecNum>155</RecNum><DisplayText>[44]</DisplayText><record><rec-number>155</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512050719">155</key><key app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Reynaud, E. G.</author><author>Krzic, U.</author><author>Greger, K.</author><author>Stelzer, E. H.</author></authors></contributors><auth-address>Cell Biology and Biophysics Unit, European Molecular Biology Laboratory (EMBL), Meyerhofstrasse 1, D-69117 Heidelberg, Germany.</auth-address><titles><title>Light sheet-based fluorescence microscopy: more dimensions, more photons, and less photodamage</title><secondary-title>HFSP Journal</secondary-title></titles><periodical><full-title>HFSP journal</full-title></periodical><pages>266-75</pages><volume>2</volume><number>5</number><edition>2009/05/01</edition><dates><year>2008</year><pub-dates><date>Oct</date></pub-dates></dates><isbn>1955-2068

(Print)
1955-205X (Linking)</isbn><accession-num>19404438</accession-num><urls><related-urls><url>https://www.ncbi.nlm.nih.gov/pubmed/19404438</url></related-urls></urls><custom2>PMC2639947</custom2><electronic-resource-num>10.2976/1.2974980</electronic-resource-num></record></Cite></EndNote>**}**. Illumination of the sample is planar and achieved orthogonal to the detection so that 2D images are generated instantaneously often using the new generation of scientific-CMOS cameras. By taking a whole 2D section in one “shot”, volume scanning is accelerated, enabling small and fast developmental events to be tracked during development. The technique has considerably advanced our ability to observe living organisms both live and *in situ* with, for example, the ability to track cell growth, movement and divisions of entire embryos **{** ADDIN EN.CITE <EndNote><Cite><Author>Rozbicki</Author><Year>2015</Year><RecNum>250</RecNum><DisplayText>[45]</DisplayText><record><rec-number>250</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1513156281">250</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Rozbicki, Emil</author><author>Chuai, Manli</author><author>Karjalainen, Antti I</author><author>Song, Feifei</author><author>Sang, Helen M</author><author>Martin, René</author><author>Knölker, Hans-Joachim</author><author>MacDonald, Michael P</author><author>Weijer, Cornelis J</author></authors></contributors><titles><title>Myosin II-mediated cell shape changes and cell intercalation contribute to primitive streak formation</title><secondary-title>Nature Cell Biology</secondary-title></titles><periodical><full-title>Nature cell biology</full-title></periodical><pages>397</pages><volume>17</volume><number>4</number><dates><year>2015</year></dates><urls></urls></record></Cite></EndNote>**}** or capturing the beating of a living heart **{** ADDIN EN.CITE <EndNote><Cite><Author>Mickoleit</Author><Year>2014</Year><RecNum>213</RecNum><DisplayText>[46]</DisplayText><record><rec-number>213</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512555423">213</key></foreign-

keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Mickoleit, Michaela</author><author>Schmid, Benjamin</author><author>Weber, Michael</author><author>Fahrbach, Florian O</author><author>Hombach, Sonja</author><author>Reischauer, Sven</author><author>Huisken, Jan</author></authors></contributors><titles><title>High-resolution reconstruction of the beating zebrafish heart</title><secondary-title>Nature Methods</secondary-title></titles><periodical><full-title>Nature methods</full-title></periodical><pages>919-922</pages><volume>11</volume><number>9</number><dates><year>2014</year></dates><isbn>1548-7091</isbn><urls></urls></record></Cite></EndNote>**}**. Because axial resolution in light sheet systems is not dependent upon high numerical aperture imaging objectives, they allow larger fields of view and can easily accommodate microcosms and instruments for maintaining healthy growth conditions **{** ADDIN EN.CITE <EndNote><Cite><Author>Reynaud</Author><Year>2015</Year><RecNum>214</RecNum><DisplayText>[47]</DisplayText><record><rec-number>214</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512555979">214</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Reynaud, Emmanuel G</author><author>Peychl, Jan</author><author>Huisken, Jan</author><author>Tomancak, Pavel</author></authors></contributors><titles><title>Guide to light-sheet microscopy for adventurous biologists</title><secondary-title>Nature Methods</secondary-title></titles><periodical><full-title>Nature methods</full-title></periodical><pages>30-34</pages><volume>12</volume><number>1</number><dates><year>2015</year></dates><isbn>1548-7091</isbn><urls></urls></record></Cite></EndNote>**}**. Details of the morphology and anatomy of tissues can be obtained without the use of markers **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}** and recently dynamic light scattering (biospeckle) has been used to enhance image contrast **{** ADDIN EN.CITE

<EndNote><Cite><Author>O’Callaghan</Author><Year>2018</Year><RecNum>247</RecNum><DisplayText>[50]</DisplayText><record><rec-number>247</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1513086523">247</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>O’Callaghan, Felicity E </author><author>Braga, Roberto A </author><author>Neilson, Roy</author><author>MacFarlane, Stuart A </author><author>Dupuy, Lionel X</author></authors></contributors><titles><title>New live screening of plant-nematode interactions in the rhizosphere</title><secondary-title>Scientific Reports</secondary-title></titles><periodical><full-title>Scientific reports</full-title></periodical><pages>1440</pages><volume>8</volume><dates><year>2018</year></dates><urls></urls></record></Cite></EndNote>**}**. Light sheet imaging has also been used in granular matter physics for a long time, although its application to root and soil is just emerging **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**.

Optics and microscopy also provides many ways to control and measure mechanical forces. Laser ablation for example, has long been used to understand the distribution of forces within a tissue **{** ADDIN EN.CITE <EndNote><Cite><Author>Sampathkumar</Author><Year>2014</Year><RecNum>242</RecNum><DisplayText>[53]</DisplayText><record><rec-number>242</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512939817">242</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Sampathkumar, Arun</author><author>Krupinski, Pawel</author><author>Wightman, Raymond</author><author>Milani, Pascale</author><author>Berquand, Alexandre</author><author>Boudaoud, Arezki</author><author>Hamant, Olivier</author><author>Jönsson, Henrik</author><author>Meyerowitz, Elliot M</author></authors></contributors><titles><title>Subcellular and supracellular mechanical stress

prescribes cytoskeleton behavior in Arabidopsis cotyledon pavement cells</title><secondary-title>Elife</secondary-title></titles><periodical><full-title>Elife</full-title></periodical><pages>e01967</pages><volume>3</volume><dates><year>2014</year></dates><isbn>2050-084X</isbn><urls></urls></record></Cite></EndNote>**}**, whilst optical trapping has been used to apply small localised forces **{** ADDIN EN.CITE <EndNote><Cite><Author>Mártonfalvi</Author><Year>2017</Year><RecNum>215</RecNum><DisplayText>[54]</DisplayText><record><rec-number>215</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512557308">215</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Mártonfalvi, Zsolt</author><author>Bianco, Pasquale</author><author>Naftz, Katalin</author><author>Ferenczy, György G</author><author>Kellermayer, Miklós</author></authors></contributors><titles><title>Force generation by titin folding</title><secondary-title>Protein Science</secondary-title></titles><periodical><full-title>Protein Science</full-title></periodical><dates><year>2017</year></dates><isbn>1469-896X</isbn><urls></urls></record></Cite></EndNote>**}**. Photoelastic materials have been central to establishing the nature of the chains of forces and how they propagate within a granular medium **{** ADDIN EN.CITE <EndNote><Cite><Author>Tordesillas</Author><Year>2014</Year><RecNum>26</RecNum><DisplayText>[55]</DisplayText><record><rec-number>26</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1511963768">26</key><key app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Tordesillas, A.</author><author>Steer, C. A. H.</author><author>Walker, D. M.</author></authors></contributors><titles><title>Force chain and contact cycle evolution in a dense granular material under shallow penetration</title><secondary-title>Nonlinear Processes in Geophysics</secondary-title></titles><periodical><full-title>Nonlinear Processes in Geophysics</full-title></periodical><pages>505-519</pages><volume>21</volume><number>2</number><section>505</section><dates><year>2014

</year></dates><isbn>1607-7946</isbn><urls></urls><electronic-resource-num>10.5194/npg-21-505-2014</electronic-resource-num></record></Cite></EndNote>}. { ADDIN EN.CITE <EndNote><Cite AuthorYear="1"><Author>Kolb</Author><Year>2012</Year><RecNum>40</RecNum><DisplayText> Kolb, et al. [56]</DisplayText><record><rec-number>40</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1511963828">40</key><key app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Kolb, Evelyne</author><author>Hartmann, Christian</author><author>Genet, Patricia</author></authors></contributors><titles><title>Radial force development during root growth measured by photoelasticity</title><secondary-title>Plant and Soil</secondary-title></titles><periodical><full-title>Plant and Soil</full-title></periodical><pages>19-35</pages><volume>360</volume><number>1-2</number><section>19</section><dates><year>2012</year></dates><isbn>0032-079X
1573-5036</isbn><urls></urls><electronic-resource-num>10.1007/s11104-012-1316-2</electronic-resource-num></record></Cite></EndNote>} used photoelasticity to characterise the forces created by root growth within a pore, and { ADDIN EN.CITE <EndNote><Cite AuthorYear="1"><Author>Wendell</Author><Year>2011</Year><RecNum>36</RecNum><DisplayText>Wendell, et al. [57]</DisplayText><record><rec-number>36</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1511963807">36</key><key app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Wendell, D.M.</author><author>Luginbuhl, K.</author><author>Guerrero, J.</author><author>Hosoi, A.E.</author></authors></contributors><titles><title>Experimental Investigation of Plant Root Growth Through Granular Substrates</title><secondary-title>Experimental Mechanics</secondary-title></titles><periodical><full-title>Experimental Mechanics</full-title></periodical><pages>945-949</pages><volume>52</volume><number>7</number><section>945</section><dates><year>2011</year></dates><isbn>0014-4851
1741-2765</isbn><urls></urls><electronic-resource-

num>10.1007/s11340-011-9569-x</electronic-resource-num></record></Cite></EndNote>**}** have successfully created a granular medium using a photo elastic media where maximum growth forces and avoidance mechanisms could be observed (Figure 1B). New cantilever-based optical sensors **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}** have also been developed to measure simultaneously growth forces generated by a root and three-dimensional strain rate in responses to changes in external forces applied to the root. **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}** for example, obtained stereoscopic data to decompose root response to axial mechanical forces into different phases (Figure 1C). Hydrogels can also be combined with fluorescent dyes and light sheet imaging to reconstruct interparticle forces within the granular medium **{** ADDIN EN.CITE <EndNote><Cite><Author>Brodu</Author><Year>2015</Year><RecNum>15</RecNum><DisplayText>[60]</DisplayText><record><rec-number>15</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1511963725">15</key><key app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Brodu, N.</author><author>Dijksman, J. A.</author><author>Behringer, R. P.</author></authors></contributors><auth-address>1] Department of Physics, Duke University, Physics Building, Science Drive, Box 90305, Durham, North Carolina 27708, USA [2] Institut National de Recherche en Informatique et en Automatique, Bordeaux Sud-Ouest, 200 avenue de la Vieille Tour, 33405 Talence, France.
1] Department of Physics, Duke University, Physics Building, Science Drive, Box 90305, Durham, North Carolina 27708, USA [2] Laboratory of Physical Chemistry and Colloid Science, Wageningen University, PO Box 8038, 6700EK Wageningen, The Netherlands.
Department of Physics, Duke University, Physics Building, Science Drive, Box 90305, Durham, North Carolina 27708, USA.</auth-address><titles><title>Spanning the scales of granular materials through microscopic force imaging</title><secondary-title>Nature Communication</secondary-title></titles><periodical><full-title>Nature Communication</full-title></periodical><pages>6361</pages><volume>6</volume><edition>2015/03/06</edition><date

s><year>2015</year><pub-dates><date>Mar 5</date></pub-dates></dates><isbn>2041-1723 (Electronic)
2041-1723 (Linking)</isbn><accession-num>25739968</accession-num><urls><related-urls><url>https://www.ncbi.nlm.nih.gov/pubmed/25739968</url></related-urls></urls><custom2>PMC4366509</custom2><electronic-resource-num>10.1038/ncomms7361</electronic-resource-num></record></Cite></EndNote>}.

Techniques for mimicking soil physical conditions under a microscope are also emerging rapidly. Transparent artificial media based on fluoropolymers that can mimic soil properties have been developed { ADDIN EN.CITE <EndNote><Cite><Author>Downie</Author><Year>2012</Year><RecNum>126</RecNum><DisplayText>[42]</DisplayText><record><rec-number>126</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1511964229">126</key><key app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Downie, H.</author><author>Holden, N.</author><author>Otten, W.</author><author>Spiers, A. J.</author><author>Valentine, T. A.</author><author>Dupuy, L. X.</author></authors></contributors><auth-address>The James Hutton Institute, Invergowrie, Dundee, United Kingdom.</auth-address><titles><title>Transparent soil for imaging the rhizosphere</title><secondary-title>PLoS One</secondary-title></titles><periodical><full-title>PLoS One</full-title></periodical><pages>e44276</pages><volume>7</volume><number>9</number><edition>2012/09/18</edition><keywords><keyword>Bacteria/metabolism</keyword><keyword>Humans</keyword><keyword>Imaging, Three-Dimensional/*methods</keyword><keyword>Microscopy, Confocal</keyword><keyword>Plant Roots/growth & development/microbiology</keyword><keyword>Refractometry</keyword><keyword>*Rhizosphere</keyword><keyword>*Soil</keyword><keyword>Soil Microbiology</keyword><keyword>Tomography</keyword></keywords><dates><year>2012</year></dates><isbn>1932-6203 (Electronic)
1932-6203 (Linking)</isbn><accession-

num>22984484</accession-num><urls><related-urls><url>https://www.ncbi.nlm.nih.gov/pubmed/22984484</url></related-urls></urls><custom2>PMC3439476</custom2><electronic-resource-num>10.1371/journal.pone.0044276</electronic-resource-num></record></Cite></EndNote>**}**. The media reproduces the physical and chemical properties of soil through control of the distribution of sizes and surface chemistry of the particles (Figure 1D). Because the particles are made of fluoropolymers that have refractive index close to water, only small adjustment of refractive indices, usually by adding a colloid to the nutrient solution, allows light to travel without refraction through the substrate. Microfluidics techniques have also progressed significantly and are becoming suitable to live and high resolution microscopy of roots and microbes **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. Microfluidics allows precise and repeatable control of liquids and this could be used, for example, to control water tension and particle cohesion in soil during live experiments. The range of materials and fabrication techniques has been considerably expanded with the use of 3D printing **{** ADDIN EN.CITE <EndNote><Cite><Author>Kitson</Author><Year>2012</Year><RecNum>216</RecNum><DisplayText>[63]</DisplayText><record><rec-number>216</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512558498">216</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Kitson, Philip J</author><author>Rosnes, Mali H</author><author>Sans, Victor</author><author>Dragone, Vincenza</author><author>Cronin, Leroy</author></authors></contributors><titles><title>Configurable 3D-Printed millifluidic and microfluidic ‘lab on a chip’reactionware devices</title><secondary-title>Lab on a Chip</secondary-title></titles><periodical><full-title>Lab on a Chip</full-title></periodical><pages>3267-3271</pages><volume>12</volume><number>18</number><dates><year>2012</year></dates><urls></urls></record></Cite></EndNote>**}**, photo lithography **{** ADDIN EN.CITE <EndNote><Cite><Author>Yanagisawa</Author><Year>2017</Year><RecNum>252</RecNum><Disp

layText>[64]</DisplayText><record><rec-number>252</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1513159699">252</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Yanagisawa, Naoki</author><author>Sugimoto, Nagisa</author><author>Arata, Hideyuki</author><author>Higashiyama, Tetsuya</author><author>Sato, Yoshikatsu</author></authors></contributors><titles><title>Capability of tip-growing plant cells to penetrate into extremely narrow gaps</title><secondary-title>Scientific Reports</secondary-title></titles><periodical><full-title>Scientific reports</full-title></periodical><pages>1403</pages><volume>7</volume><number>1</number><dates><year>2017</year></dates><isbn>2045-2322</isbn><urls></urls></record></Cite></EndNote>**}**, etching technics **{** ADDIN EN.CITE <EndNote><Cite><Author>Anderson</Author><Year>2000</Year><RecNum>217</RecNum><DisplayText>[65]</DisplayText><record><rec-number>217</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512558714">217</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Anderson, Janelle R</author><author>Chiu, Daniel T</author><author>Wu, Hongkai</author><author>Schueller, OJ</author><author>Whitesides, George M</author></authors></contributors><titles><title>Fabrication of microfluidic systems in poly (dimethylsiloxane)</title><secondary-title>Electrophoresis</secondary-title></titles><periodical><full-title>Electrophoresis</full-title></periodical><pages>27-40</pages><volume>21</volume><number>1</number><dates><year>2000</year></dates><urls></urls></record></Cite></EndNote>**}** and the use of optically controlled fluidics **{** ADDIN EN.CITE <EndNote><Cite><Author>Neale</Author><Year>2005</Year><RecNum>218</RecNum><DisplayText>[66,67]</DisplayText><record><rec-number>218</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512558942">218</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Neale,

Steven L</author><author>MacDonald, Michael P</author><author>Dholakia, Kishan</author><author>Krauss, Thomas F</author></authors></contributors><titles><title>All-optical control of microfluidic components using form birefringence</title><secondary-title>Nature Materials</secondary-title></titles><periodical><full-title>Nature Materials</full-title></periodical><pages>530-533</pages><volume>4</volume><number>7</number><dates><year>2005</year></dates><isbn>1476-1122</isbn><urls></urls></record></Cite><Cite><Author>Baret</Author><Year>2009</Year><RecNum>219</RecNum><record><rec-number>219</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512558970">219</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Baret, Jean-Christophe</author><author>Miller, Oliver J</author><author>Taly, Valerie</author><author>Ryckelynck, Michaël</author><author>El-Harrak, Abdeslam</author><author>Frenz, Lucas</author><author>Rick, Christian</author><author>Samuels, Michael L</author><author>Hutchison, J Brian</author><author>Agresti, Jeremy J</author></authors></contributors><titles><title>Fluorescence-activated droplet sorting (FADS): efficient microfluidic cell sorting based on enzymatic activity</title><secondary-title>Lab on a Chip</secondary-title></titles><periodical><full-title>Lab on a Chip</full-title></periodical><pages>1850-1858</pages><volume>9</volume><number>13</number><dates><year>2009</year></dates><urls></urls></record></Cite></EndNote>**}**. It has been possible, for example, to produce chambers with physical heterogeneity, physical barriers and chemical gradients, with direct applications to root and soil studies **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}** .

The scientific community is better equipped than ever to make observations on the micromechanics of root development in soil. Experimental systems provide soil-like growth conditions and allow for observations, measurements and data generation with precision, accuracy and resolution. How then to transform the amount of information available to us into scientific breakthrough? The complexity of the root-particle interactions is a major challenge. At each growth step, a root is in contact with a new arrangement of particles that apply forces of varying magnitudes and orientations. Because there are countless numbers of possible arrangements, the forces applied on roots cannot be experimentally controlled. Measurements of granular forces *in situ* is required (Figure 2.1), and granular media physicist have achieved such measurements. There are now great opportunities to combine current knowledge of soil micromechanics with mechanobiology and propose a mechanistic framework that account for sensing and response to micro-scale heterogeneity (Figure 2.2). New theories must be developed to embrace stochasticity and explain responses to multiple mechanical stimuli (Figure 2.3-4). Major challenges remain, but a recent look at the literature indicates our thinking is evolving in the right way.

Figures

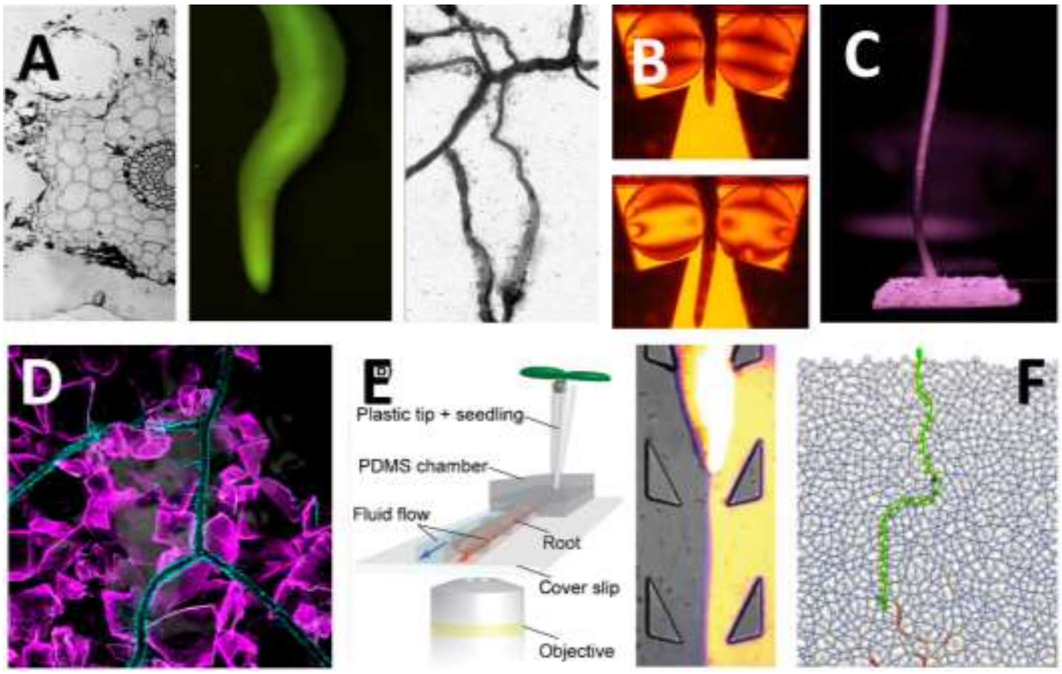
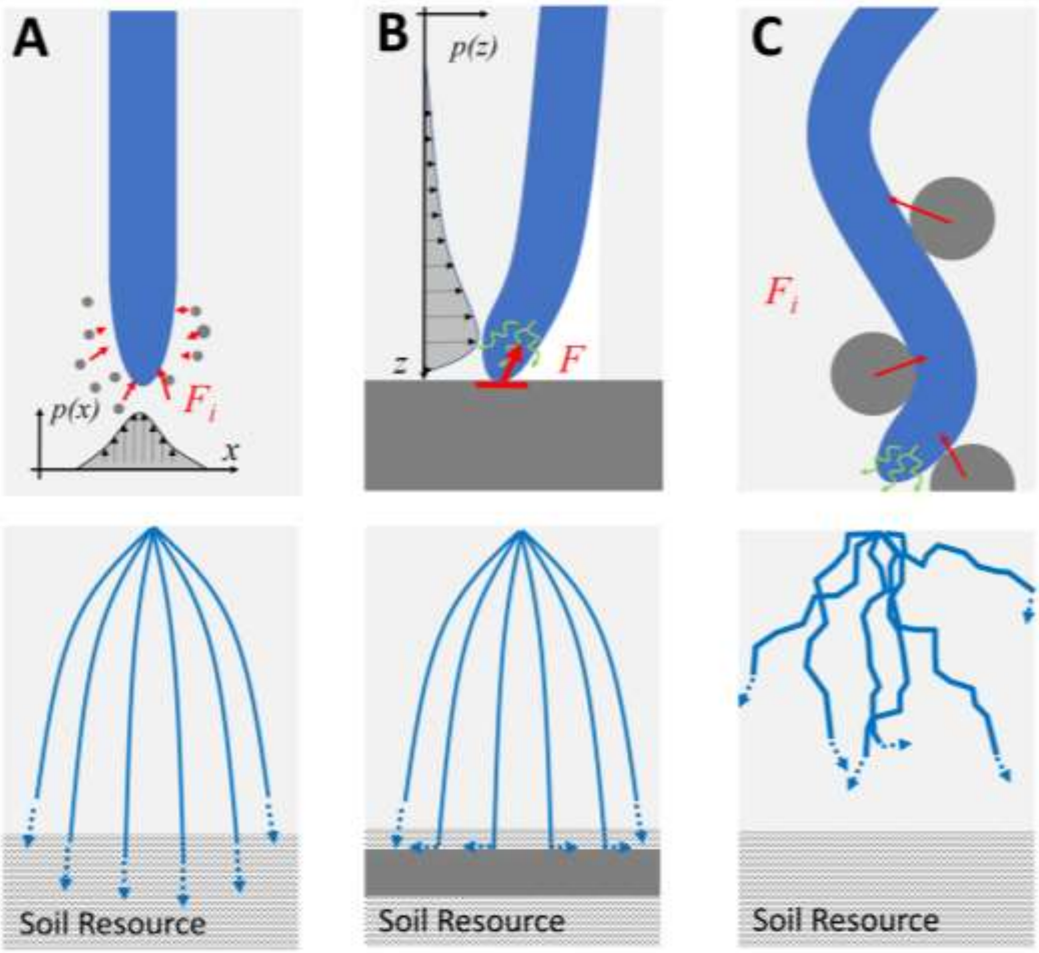


Figure 1: Growing roots interact mechanically with soil particles during growth. These interactions influence the morphology of the root, and the dynamics of development of the root system. A) Irregular growth of cortex cells is observed in hard or compacted soil { ADDIN EN.CITE <EndNote><Cite><Author>Lipiec</Author><Year>2012</Year><RecNum>243</RecNum><Prefix>left `, </Prefix><DisplayText>[left, 69]</DisplayText><record><rec-number>243</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1513078014">243</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Lipiec, Jerzy</author><author>Horn, Rainer</author><author>Pietrusiewicz, Jacek</author><author>Siczek, Anna</author></authors></contributors><titles><title>Effects of soil compaction on root elongation and anatomy of different cereal plant species</title><secondary-title>Soil and Tillage Research</secondary-title></titles><periodical><full-title>Soil and Tillage Research</full-title></periodical><pages>74-81</pages><volume>121</volume><dates><year>2012</year></dates><isbn>0167-1987</isbn><urls></urls></record></Cite></EndNote>}. Resistance from the soil particles causes

root diameter to increase and the root tip to buckle and bend towards the path of least resistance (middle, lentils roots grown at 2MPa confining pressure). At the scale of the root system, interactions causes growth trajectories to be stochastic as observed here on *Anthyllis vulneraria* grown on landslide soils (image courtesy Loïc Pagès). Technological developments now allow precise characterisation of mechanical interactions between a root and the growth substrate. These include for example, B) photoelastic discs for measurement of growth forces in soil pores **{** ADDIN EN.CITE <EndNote><Cite><Author>Kolb</Author><Year>2012</Year><RecNum>40</RecNum><DisplayText>[56]</DisplayText><record><rec-number>40</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1511963828">40</key><key app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Kolb, Evelyne</author><author>Hartmann, Christian</author><author>Genet, Patricia</author></authors></contributors><titles><title>Radial force development during root growth measured by photoelasticity</title><secondary-title>Plant and Soil</secondary-title></titles><periodical><full-title>Plant and Soil</full-title></periodical><pages>19-35</pages><volume>360</volume><number>1-2</number><section>19</section><dates><year>2012</year></dates><isbn>0032-079X
1573-5036</isbn><urls></urls><electronic-resource-num>10.1007/s11104-012-1316-2</electronic-resource-num></record></Cite></EndNote>**}** (images courtesy Evelyne Kolb), C) root growing on a cantilever sensor for measuring growth forces **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**, D) transparent soil substrates that provide the physical structure of soil with the ability to carry out 3D live imaging **{** ADDIN EN.CITE <EndNote><Cite><Author>O’Callaghan</Author><Year>2018</Year><RecNum>247</RecNum><DisplayText>[50]</DisplayText><record><rec-number>247</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1513086523">247</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>O’Callaghan, Felicity E </author><author>Braga, Roberto A </author><author>Neilson, Roy</author><author>MacFarlane, Stuart A </author><author>Dupuy, Lionel X</author></authors></contributors><titles><title>New live screening of plant-nematode interactions in the rhizosphere</title><secondary-title>Scientific Reports</secondary-title></titles><periodical><full-title>Scientific reports</full-title></periodical><pages>1440</pages><volume>8</volume><dates><year>2018</year></dates><urls></urls></record></Cite></EndNote>**}**, E) Dual flow microfluidic systems with microscale both physical and nutrient heterogeneity **{** ADDIN EN.CITE <EndNote><Cite><Author>Stanley</Author><Year>2018</Year><RecNum>261</RecNum><DisplayText>[68]</DisplayText><record><rec-number>261</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1518642710">261</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Stanley, Claire E</author><author>Shrivastava, Jagriti</author><author>Brugman, Rik</author><author>Heinzelmann, Elisa</author><author>Swaay, Dirk</author><author>Grossmann, Guido</author></authors></contributors><titles><title>Dual-flow-RootChip reveals local adaptations of roots towards environmental asymmetry at the physiological and genetic levels</title><secondary-title>New Phytologist</secondary-title></titles><periodical><full-title>New Phytologist</full-title></periodical><pages>1357-1369</pages><volume>217</volume><number>3</number><dates><year>2018</year></dates><isbn>1469-8137</isbn><urls></urls></record></Cite></EndNote>**}** and F) discrete element modelling for testing root responses to interactions with granular media **{** ADDIN EN.CITE <EndNote><Cite><Author>Fakih</Author><Year>2017</Year><RecNum>270</RecNum><DisplayText>[28]</DisplayText><record><rec-number>270</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1520156221">270</key></foreign-keys><ref-type name="Conference Proceedings">10</ref-type><contributors><authors><author>Fakih, Mahmoud</author><author>Delenne, Jean Yves</author><author>Radjai, Farhang</author><author>Fourcaud,

Thierry</author></authors></contributors><titles><title>Modeling root growth in granular soils: effects of root stiffness and packing fraction</title><secondary-title>EPJ Web of Conferences</secondary-title></titles><periodical><full-title>EPJ Web of Conferences</full-title></periodical><pages>14013</pages><volume>140</volume><dates><year>2017</year></dates><publisher>EDP Sciences</publisher><isbn>2100-014X</isbn><urls></urls></record></Cite></EndNote>**}** (image courtesy Mahmoud Fakih).



Box 1: Root primary growth is a local process where elongation of tissues is taking place at the root tip. Soil heterogeneity influences strongly how the tissue elongates and deforms (top), and local interactions taking place at the tip can have drastic effects on the morphology and development of the

whole root system, and the resources available to the plant (bottom). Mathematical modelling provides a useful framework to explain how heterogeneity can affect the morphology of the root system.

(A) When roots grow in soil particles which representative volume is small compared to the diameter of the roots, the action of the particles can be averaged (top). In such conditions, it is unlikely for a plant to perceive the fluctuations of forces from individual particles. If the mechanical resistance of the soil is not limiting, root trajectories follow smooth streamlines (bottom). Mathematically, this phenomenon has been described as the convection of root tips (density ρ) **{** *ADDIN EN.CITE <EndNote><Cite><Author>Kalogiros</Author><Year>2016</Year><RecNum>241</RecNum><DisplayText>[70]</DisplayText><record><rec-number>241</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512938995">241</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Kalogiros, Dimitris I</author><author>Adu, Michael O</author><author>White, Philip J</author><author>Broadley, Martin R</author><author>Draye, Xavier</author><author>Ptashnyk, Mariya</author><author>Bengough, A Glyn</author><author>Dupuy, Lionel X</author></authors></contributors><titles><title>Analysis of root growth from a phenotyping data set using a density-based model</title><secondary-title>Journal of Experimental Botany</secondary-title></titles><periodical><full-title>Journal of experimental botany</full-title></periodical><pages>1045-1058</pages><volume>67</volume><number>4</number><dates><year>2016</year></dates><isbn>0022-0957</isbn><urls></urls></record></Cite></EndNote>***}****. The growth velocity E (cm.d^{-1}) and the rate of change in root angle due to gravitropism g (d^{-1}) define the growth of the root system:*

$$\partial_t \rho + \nabla \cdot \mathrm{F} + \partial_\theta g \rho = 0,$$

with $\mathrm{F} = \rho E(\cos(\theta) + \sin(\theta))$ is the spatial flux of root tips and $g\rho$ is the angular flux of roots. In this case, growth and resource acquisition is optimal.

(B) When soil elements cannot be displaced, in the case of stones and rock for example, the root adopts avoidance behaviours. Optimal growth is not affected and remains similar to (A), until the obstacle is reached. Heterogeneities in this case define the boundaries within which convective growth is taking place. Using the same mathematical framework, presence of such boundaries can be modelled through boundary conditions, for example

$$\partial_n \rho = 0.$$

Large scale soil heterogeneities can be problematic because they may restrain access to pools of resources, e.g. deep water, even though the root growth in most parts of the soil domain is unaffected. They may also forms paths of least growth resistance, for example in the case of pores and cracks.

(C) Intermediate cases are more problematic to analyse. Roots are in contact with particles which apply forces of varying magnitudes and orientation. Although the root may overcome these forces, a single particle may be able to deflect the growth trajectory. Since particles have inhomogeneous distribution, root deflection occurs is stochastic. Mathematically, the phenomenon can be described by a convection, where the growth velocity e<E (cm.d^{-1}) and the rate of change in root angle due to gravitropism g (d^{-1}) and random fluctuations define the dynamics:

$$\partial_t \rho + \nabla \cdot \mathrm{F} + \partial_\theta (g\rho + D\partial_\theta \rho) = 0,$$

$g\rho + D\partial_\theta \rho$ the angular flux of roots. The parameter D is the angular diffusion coefficient. Because D relates to the probability of roots to be deflected by a particle, and the magnitude of such deflection, there is a direct link between micro-mechanics of root particle interactions and the morphology of the root system. Diffusive growth makes root trajectories irregular, and limits the expansion of the root system, even when the elongation rate is not affected. Mathematical analysis of equation 3 reveals the conditions for which transitions from convective growth to diffusive growth occur, i.e. for Peclet number $P_e = \frac{g}{D} \ll 1$.

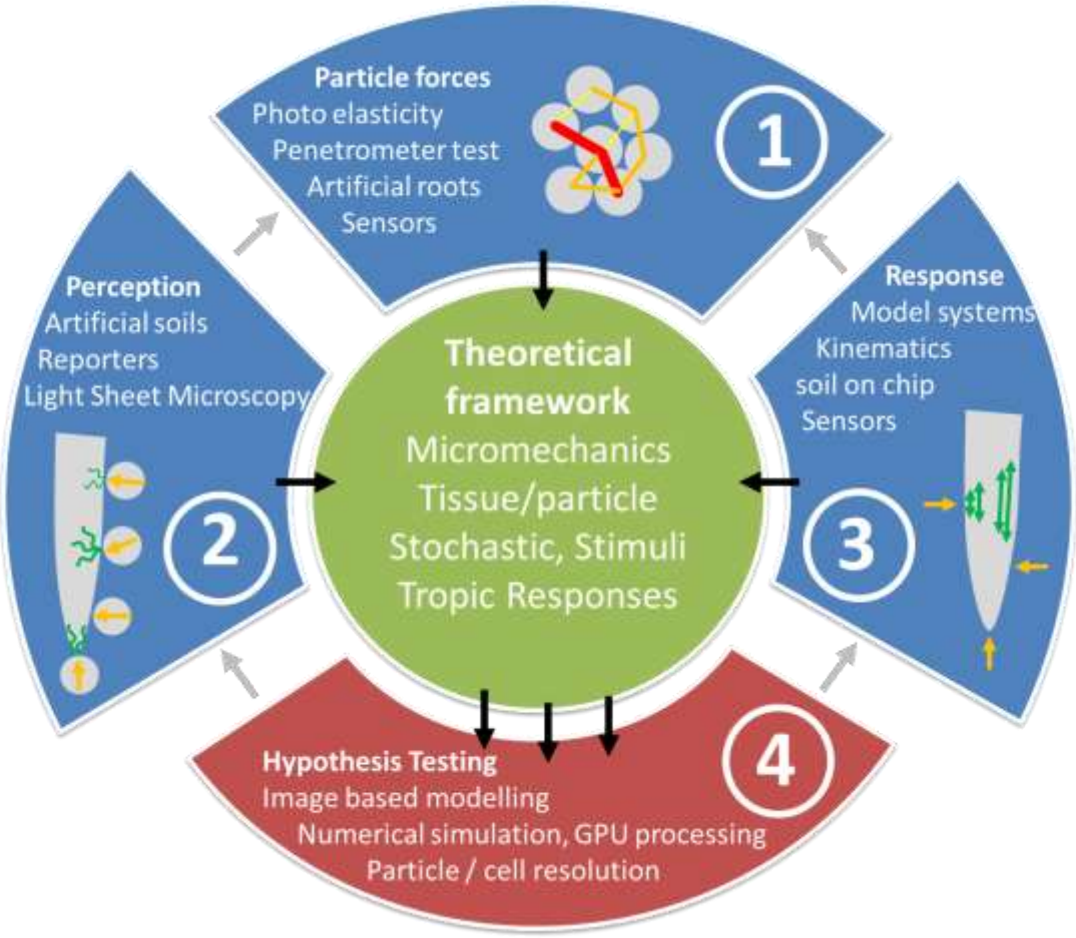


Figure 2: Dissecting the complexity of root particles mechanical interactions requires an elaborate research strategy. (1) First step is to better understand the nature of the forces applied to a root. This can be achieved, using photo elastic beads, imaging, or developing artificial roots equipped with sensors { ADDIN EN.CITE <EndNote><Cite><Author>Sadeghi</Author><Year>2016</Year><RecNum>248</RecNum><DisplayText>[71]</DisplayText><record><rec-number>248</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1513096573">248</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Sadeghi, Ali</author><author>Mondini, Alessio</author><author>Del Dottore, Emanuela</author><author>Mattoli, Virgilio</author><author>Beccai, Lucia</author><author>Taccola, Silvia</author><author>Lucarotti, Chiara</author><author>Totaro, Massimo</author><author>Mazzolai, Barbara</author></authors></contributors><titles><title>A

plant-inspired robot with soft differential bending capabilities</title><secondary-title>Bioinspiration & biomimetics</secondary-title></titles><periodical><full-title>Bioinspiration & biomimetics</full-title></periodical><pages>015001</pages><volume>12</volume><number>1</number><dates><year>2016</year></dates><isbn>1748-3190</isbn><urls></urls></record></Cite></EndNote>**}**, but also by revisiting older techniques, for example by analysing micro penetrometer test and exploit force fluctuations **{** ADDIN EN.CITE <EndNote><Cite><Author>Perfect</Author><Year>1990</Year><RecNum>249</RecNum><DisplayText>[72]</DisplayText><record><rec-number>249</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1513096878">249</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Perfect, E</author><author>Groenevelt, PH</author><author>Kay, BD</author><author>Grant, CD</author></authors></contributors><titles><title>Spatial variability of soil penetrometer measurements at the mesoscopic scale</title><secondary-title>Soil and Tillage Research</secondary-title></titles><periodical><full-title>Soil and Tillage Research</full-title></periodical><pages>257-271</pages><volume>16</volume><number>3</number><dates><year>1990</year></dates><isbn>0167-1987</isbn><urls></urls></record></Cite></EndNote>**}**. (2) In the second step, it is essential to characterise how these forces (orange arrows) are perceived by plant roots. This could be achieved using e.g. modern LSM microscopes, artificial soils, calcium or FRET tension sensors to inform on the perception of forces induced by heterogeneous media **{** ADDIN EN.CITE <EndNote><Cite><Author>Monshausen</Author><Year>2012</Year><RecNum>254</RecNum><DisplayText>[73]</DisplayText><record><rec-number>254</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1513160863">254</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Monshausen, Gabriele B</author></authors></contributors><titles><title>Visualizing Ca 2+ signatures in

plants</title><secondary-title>Current Opinion in Plant Biology</secondary-title></titles><periodical><full-title>Current opinion in plant biology</full-title></periodical><pages>677-682</pages><volume>15</volume><number>6</number><dates><year>2012</year></dates><isbn>1369-5266</isbn><urls></urls></record></Cite></EndNote>**}**. (3) Finally, the mechanism of response to complex distribution of forces must be characterised. In this case, responses can be studied on simplified systems where position and magnitude of forces can be controlled accurately, using lab-on-chip device and more traditional developmental biology approaches. Experiments and data can then be used to formulate and test new concepts and biomechanical theories (black arrows). Computational models can test biomechanical theories in most realistic conditions using latest technologies, e.g. particle based simulations and computer hardware (4) and influence the design of new experiments (grey arrows).

Acknowledgements

This work was supported by the consolidator fellowship from the European Research Council ERC SENSOILS-647857. We also thank the colleagues from the RoSoM project for inspiring discussions on root biomechanics and discrete element modelling (Agropolis Fondation ID 1202-073; LabexAgro: ANR-10-LABX- 001-01).

Publication Highlight

9. Bengough AG, Loades K, McKenzie BM: **Root hairs aid soil penetration by anchoring the root surface to pore walls**. *Journal of Experimental Botany* 2016, **67**:1071-1078.

This paper demontrates that penetration of granular media uses root hair cells to anchor the base of the root while the tip of the root is moving and expanding. The study provides experimental evidence that root microscopic traits play an important role in mechanical interactions with the granular media.

10. Colombi T, Kirchgessner N, Walter A, Keller T: **Root tip shape governs root elongation rate under increased soil strength**. *Plant Physiology* 2017, **174**:2289-2301.

This study illustrates the role of the morphology of the root tip in the penetration of hard soil. The angle of the root tip, more than the diameter itself, is found to be the trait that segregates for ability to overcome mechanical resistance from soil in a set of wheat genotypes.

11. Kolb E, Legue V, Bogeat-Triboulot M-B: **Physical root-soil interactions**. *Physical Biology* 2017, **14**:065004.

This paper provides an overview of the physics of root soil interactions. The study classify the main biomechanical processes of growth, namely axial elongation, thickening and reorientation, and it details the basic principles that control their magnitude and occurrence in a soil.

19. Hurley R, Hall S, Andrade J, Wright J: **Quantifying interparticle forces and heterogeneity in 3D granular materials**. *Physical Review Letters* 2016, **117**:098005.
This paper provides a clear and concise introductions to current understanding of granular matter physics and demonstrates how modern imaging techniques can lead to detailed quantification of interparticle forces in a granular medium.

28. Fakih M, Delenne JY, Radjai F, Fourcaud T: **Contribution of mechanical factors to the variability of root architecture: Quantifying the past history of interaction forces between growing roots and soil grains**. In *2016 IEEE International Conference on Functional-Structural Plant Growth Modeling, Simulation, Visualization and Applications (FSPMA)*. Edited by; 2016:52-60.
This is the first modelling study of root growth in a soil represented at the microscopic scale. The work also presents interesting preliminary results showing factors that contribute to the stabilty of root trajectories and the nature of particle forces that develop in response to growth.

30. Hamilton ES, Schlegel AM, Haswell ES: **United in diversity: mechanosensitive ion channels in plants**. *Annual Review of Plant Biology* 2015, **66**:113-137.
This paper reviews current knowledge on mechanosensitive ion channels, and how these are though to link to plant perception and response to mechanical force.

37. Keyes S, Cooper L, Duncan S, Koebernick N, Fletcher DM, Scotson C, Van Veelen A, Sinclair I, Roose T: **Measurement of micro-scale soil deformation around roots using four-dimensional synchrotron tomography and image correlation**. *Journal of The Royal Society Interface* 2017, **14**:20170560.

This paper exposes state of the art approaches to track plant growth and particle movement in soil. The study combines synchrotron based X-Ray tomography with image corelation to estimate soil displacement around the root.

44. Reynaud EG, Peychl J, Huisken J, Tomancak P: **Guide to light-sheet microscopy for adventurous biologists**. *Nature Methods* 2015, **12**:30-34.
This is an introduction to light-sheet microscopy for beginers. It covers aspects related to basic principles, existing commercial device, and data generation and hadling process.

50. O'Callaghan FE, Braga RA, Neilson R, MacFarlane SA, Dupuy LX: **New live screening of plant-nematode interactions in the rhizosphere**. *Scientific Reports* 2018, **8**:1440
This study demonstrates the use of transparent soil and light sheet microscopy to study root-particle-nematode ineractions. The paper combines dynamic speckle and light sheet imaging to enhance the contrast of microscopic worms without the need for fluorescent labelling.

59. Bizet F, Bengough AG, Hummel I, Bogeat-Triboulot MB, Dupuy LX: **3D deformation field in growing plant roots reveals both mechanical and biological responses to axial mechanical forces**. *Journal of Experimental Botany* 2016, **67**:5605-5614.
This study presents the development of cantilever based mechanical sensor to assess growth forces of a root on an obstacle simultaneously with quantification of the elongation of the root tissue. The study uses stereoscopic reconstruction to determine growth responses in 3 dimensions.

60. Brodu N, Dijksman JA, Behringer RP: **Spanning the scales of granular materials through microscopic force imaging**. *Nature Communication* 2015, **6**:6361.
This study demonstrates how measurement of particle forces can be achieved in a light sheet imaging set up. The experimental system consists of deformable beads in a refractive index matched

solution. The reconstruction of the deformed shape of particles is then used to determine inter-particle forces in the granular media.

68. Stanley CE, Shrivastava J, Brugman R, Heinzelmann E, Swaay D, Grossmann G: **Dual-flow-RootChip reveals local adaptations of roots towards environmental asymmetry at the physiological and genetic levels**. *New Phytologist* 2018, **217**:1357-1369

This paper exposes the development of microfluidic devices that mimic soil heterogeneity. The study shows how asymetric phosphate distribution affects growth response of root hairs.

72. Sadeghi A, Mondini A, Del Dottore E, Mattoli V, Beccai L, Taccola S, Lucarotti C, Totaro M, Mazzolai B: **A plant-inspired robot with soft differential bending capabilities**. *Bioinspiration & biomimetics* 2016, **12**:015001.

This study explores the development of root inspired robotic devices to penetrate soil. The device embark various sensors (touch, humidity, accelerometer). Athough the work targets soil monitoring and exploration, similar devices could be used to obtain data on the nature of the force experienced by roots during growth.

References

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